

THE ROLE OF PLANT-POLLINATOR INTERACTIONS IN DETERMINING COMMUNITY STRUCTURE¹

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This paper is dedicated to the recent generation of studies on community structure that utilize systems analysis and energy flow but fail to mention, or mention only in passing, the reproductive parts of plants. Flowers and fruits are passed over because they usually represent an insignificant proportion of the standing biomass of most forests (Odum *et al.*, 1970; Fittkau & Klinge, 1973), however, we should not lose sight of the fact that for most plant species those metric tons of standing biomass are the product of the evolution of mechanisms to provide sufficient energy for the formation of propagules. Further, the formation of propagules often involves the coevolved behaviors of plants and animals. These interactions are even more difficult to express as energy gained or lost in an ecosystem. It appears that the "importance" of community subsets cannot always be measured in terms of calories.

One other expression of the importance of a set of interactions, such as plant-pollinator interactions, is its contribution to the determination of community structure. Community structure may be defined by several parameters, including species diversity and dominance patterns, trophic structure, or diversity of reproductive types. To simplify analysis, I will confine this discussion to the consideration of diversity at one trophic level, the consumers of nectar or pollen, and to one reproductive type, flowering angiosperms. The question to be considered is, how important are plant-flower-visitor interactions in determining the diversity of visitors and plants that rely on animals for reproduction?

This is an important question because there has been no clear demonstration that the structure of flower-visitor communities depends on the floral resources that are available. While it is obvious that animals such as bees are found where there is some nectar and pollen, it is not obvious that the structure of entire flower-visitor communities is largely a function of the number of flowers present and the way visitors partition the resource. There are at least three classes of theory explaining diversity differences among communities, and plant-pollinator interactions would be important in only one of these. One theory claims communities are not saturated with species and differences in diversity result from historical considerations (*e.g.* Whittaker, 1969). If flowering plant and flower-visitor species diversity are the result of historical accidents, then plant-pollinator

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interactions are important as factors in speciation but not in regulation of community diversity.

Two other classes of theory are based on the existence of an equilibrium in the number of species in a community, but they differ in the proposed regulatory mechanisms. The predation theory (Paine, 1966; Janzen, 1970) asserts that predator regulation of prey populations may increase the diversity of prey species by preventing the dominance of any single prey species. Predation may also maintain low prey diversities depending on the selectivity of the predator (Harper, 1969; Paine & Vadas, 1969). Theoretically, predation could be an important factor in regulating plant (Janzen, 1970) and flower-visitor (Elton, 1973) diversity. In this case we would conclude again that the coevolution of these groups is significant in the process of species evolution but not for the determination of community structure.

Finally, the other equilibrium theory claims that species numbers are regulated by competition among members of a community (Klopfer & MacArthur, 1960; Levins, 1968; Vandermeer, 1970; MacArthur, 1970, 1972). MacArthur (1972) considers species diversity to be a function of three factors: (1) the diversity of resources available in a community, (2) the average portion of the resources used by each species (niche breadth), and (3) the average part of each species niche that is shared with other taxa (niche overlap). Increasing the diversity of resources can increase the number of consumer species in a community maintaining a competitive equilibrium in diversity. Consumer diversity can also be increased by increasing specialization (decreasing niche breadth) or by increasing the average niche overlap in a community. If competitive interactions are widely important in determining plant or flower-visitor species numbers, then the coevolution of these groups is important both as a factor in speciation and in the regulation of community structure.

The experimental measurement of competition in complex communities is nearly impossible. To answer the question of whether competitive interactions are important in regulating species diversity we need to test the accuracy of predictions made by the "competition theory" using real communities. That is, are differences in species diversity among communities accompanied by the predicted differences in resource diversity, average niche breadth, and average niche overlap? Raven and Moldenke initiated a program to study a series of plant flower-visitor communities in California (Moldenke, 1971) and Chile. My studies were an extension of this program and included four seasonal tropical communities in Costa Rica. Some patterns are emerging on a local scale, although results from broad geographical comparisons have not been fully analyzed. I will discuss these local patterns in the Costa Rican communities for the regulation of flower-visitor diversity and then for plants that are potentially competing for pollinator services.

THE FLOWER-VISITOR "COMMUNITY"

I will only summarize the techniques used in Costa Rica, since these are reported in detail elsewhere (Heithaus, 1973). Four communities were chosen;

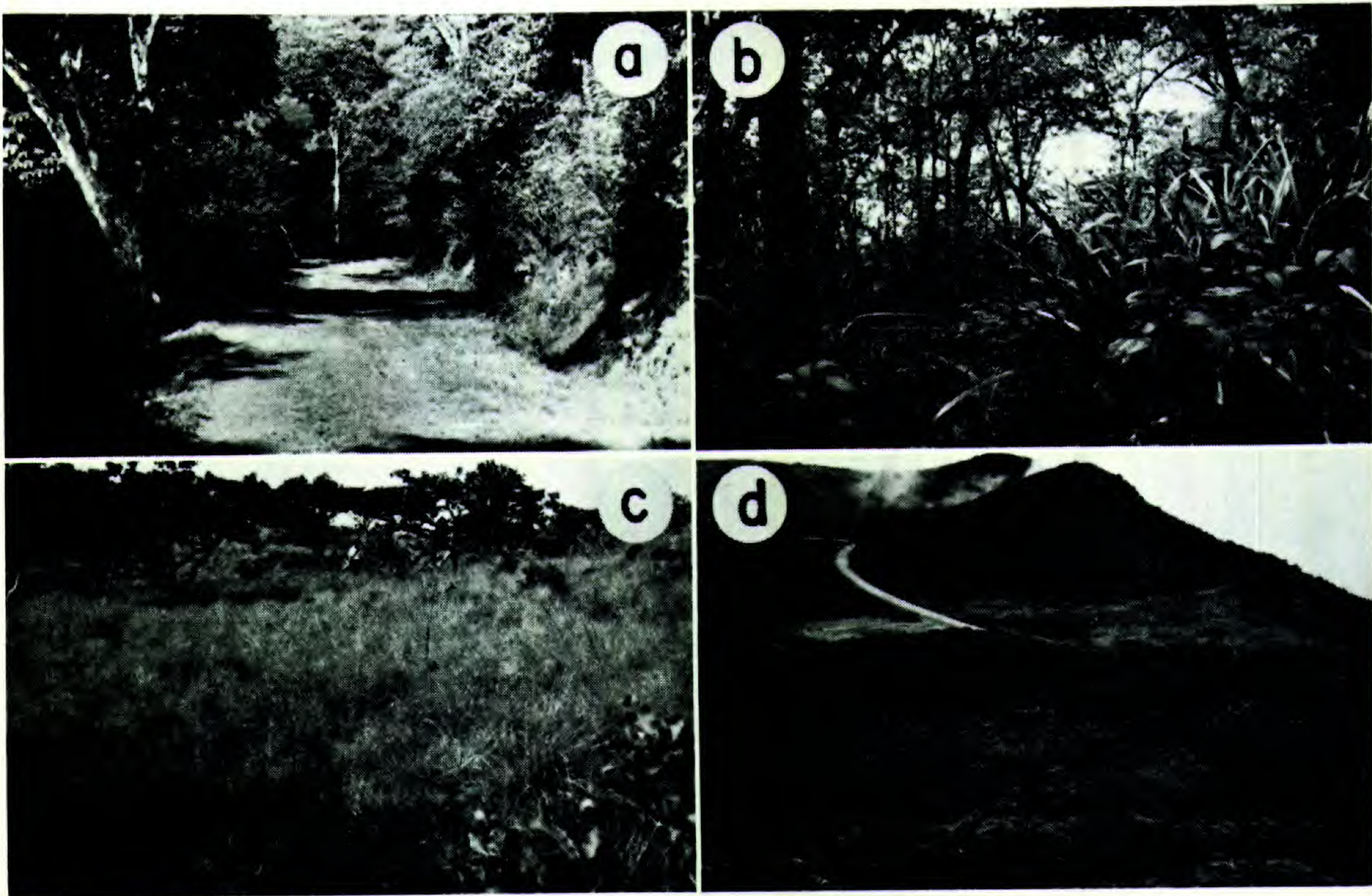


FIGURE 1. The four Costa Rican study areas.—a. Area E, a complex, lowland deciduous forest. The conspicuous tree at the end of the road is 25 m tall.—b. Area G, a “simple,” lowland deciduous forest. Note the relatively open canopy. The shrub on the right, *Bromelia pinguin*, is 1.7 m tall.—c. Area S, a grassland “savanna.” Note the figure in the center, among *Byrsonema crassifolia* trees.—d). Panorama of Area P, the montane wet rain forest site. The dominant shrubs are 2–3 m high.

three were in the Tropical Dry Forest life zone and one in the Montane Rain Forest life zone of Holdridge (1967). The communities differed in physical structure and plant diversity as seen in Figure 1. The lowland communities included a complex deciduous forest (Area E), a simple deciduous forest (Area G), and a grassland-savanna (Area S). The high altitude site (3335 m, Area P) was dominated by shrubs and was subject to frosts and occasional freezes. Monthly estimates of floral resources were made. These estimates took into account both the number and size of flowers found in quadrats and along transects. Flower visitors were observed at each site for at least one week each month. Where field identifications were reliable (*e.g.* hummingbirds and some butterflies) I did not collect the visitors, but insects were usually collected. Using over 20,000 observations of flower visitation, I calculated the niche breadth for flower visitation for each species and the pairwise niche overlap among the different species. Niche breadth and overlap were calculated using the method of Colwell and Futuyma (1971). Their method facilitates the comparison of trends in niche metrics over different communities because differences in the amount of resource and differences in resource spacing among communities are taken into account. We therefore have relatively independent estimates of niche breadth, niche overlap, and resource diversity in each of the communities. I will now discuss the observed relationship between flower-visitor diversity and each of these three parameters.

TABLE 1. The number of visitor species in the dry and wet seasons, and total visitor species numbers.

Group	Number of Species											
	Season											
	Dry				Wet				Total			
	Area				Area				Area			
	E	G	S	P	E	G	S	P	E	G	S	P
Coleoptera	42	15	5	3	80	33	12	6	107	37	12	8
Diptera ^a	22	8	7	20	35	15	7	25	46	16	9	37
Hymenoptera												
Bees	126	72	43	6	125	67	44	6	170	87	52	7
Wasps	62	47	20	1	89	49	22	6	112	6	31	7
Lepidoptera	56	25	18	13	123	46	27	4	138	51	31	6
Trochilidae	7	7	2	3	7	7	2	4	7	7	2	5
Miscellaneous	3	1	0	0	3	0	1	0	6	1	1	0
Total	318	175	95	46	462	217	115	51	586	260	138	69

^a Diptera are represented only by the families Bombyliidae, Nemestrinidae, and Tachinidae.

DIVERSITY AND NICHE BREADTH

Over 900 species in seven major taxonomic groups were observed at flowers (Table 1). The breadth of taxa included in this analysis is important. Since we are concerned with potential competition for floral resources, we should logically consider all groups that are utilizing these resources. For example, we should not analyze niche metrics for bees alone, because competition with other groups, such as hummingbirds, can influence bee feeding-patterns. One advantage of the program initiated by Raven and Moldenke is the study of ecologically determined groups.

The problem of estimating niche breadth for rare species was avoided by calculating niche breadth for only those species represented by at least 12 individuals. Unfortunately, most flower-visitor species in Costa Rica were represented by only one to eleven individuals (Fig. 2), so the estimate of mean niche breadth is from a sample of the total species pool. There was no evidence, however, that rare species were actively excluded from visiting flowers also used by common species (Heithaus, 1973). Further, the proportion of species that were rare was nearly the same for all communities, so it is likely that the niche breadth estimates are reasonably used as indicators of community interactions.

As predicted by the competition theory, there was a decrease in the mean niche breadth (or increased specialization) of common flower-visitor as the number of species in the lowland communities increased (Fig. 3). In terms of the Colwell-Futuyma measure of niche breadth, this means that each lowland flower-visitor species tended to utilize a smaller proportion of the total available resource as the number of species in the community increased. The results from the seasonal lowland areas agree with those of Moldenke (1971), who found that

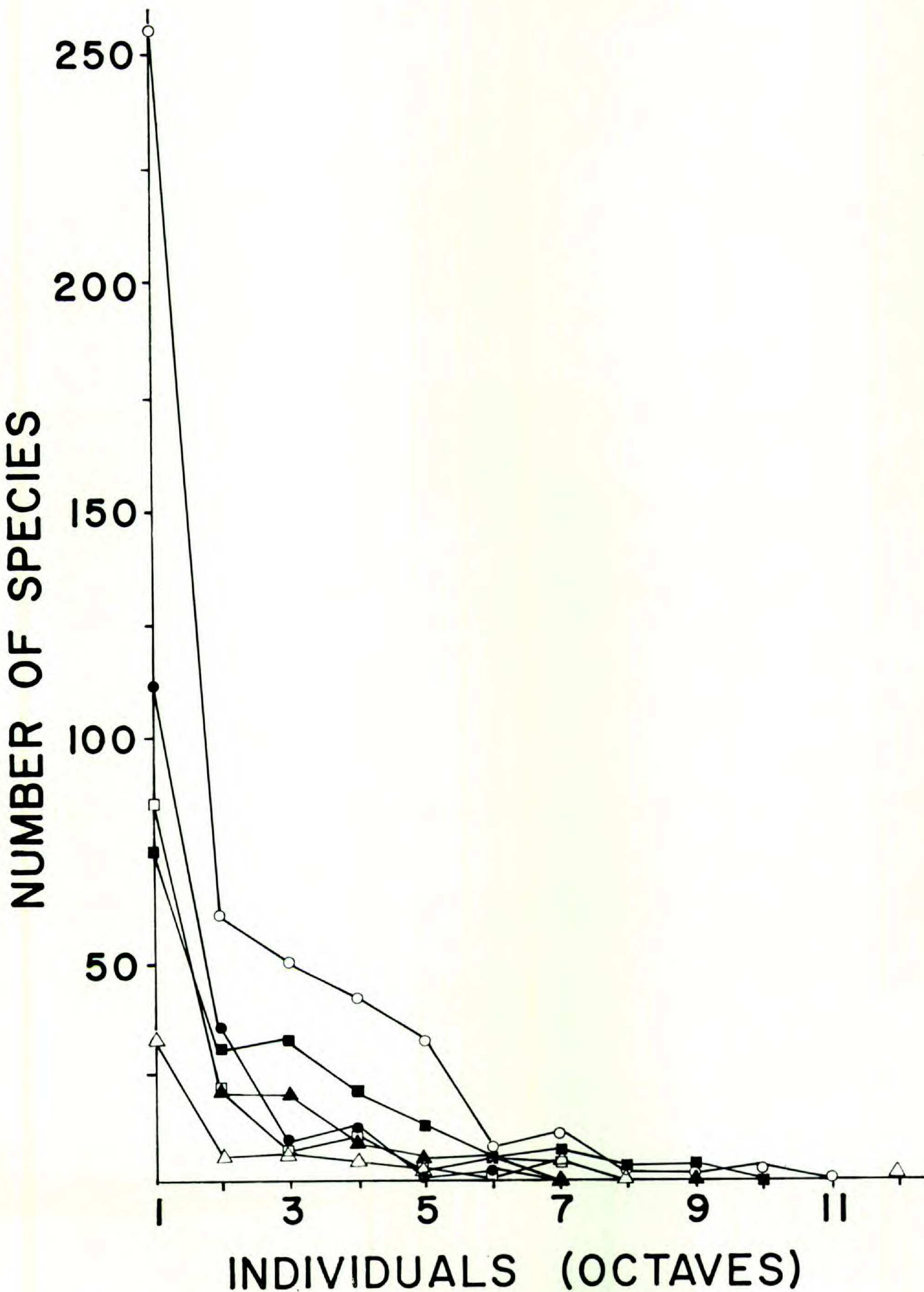


FIGURE 2. The distribution of individuals among species, plotted according to the method of Preston (1948). The number of individuals per species is given on a log₂ scale; the upper bounds of "octaves" are in the series 2⁰, 2¹, 2² . . . 2ⁿ. The ordinate gives the number of species with at least 2ⁿ individuals. ○ = Area E, wet season; ● = Area E, dry season; □ = Area G, wet season; ■ = Area S; △ = Area P.

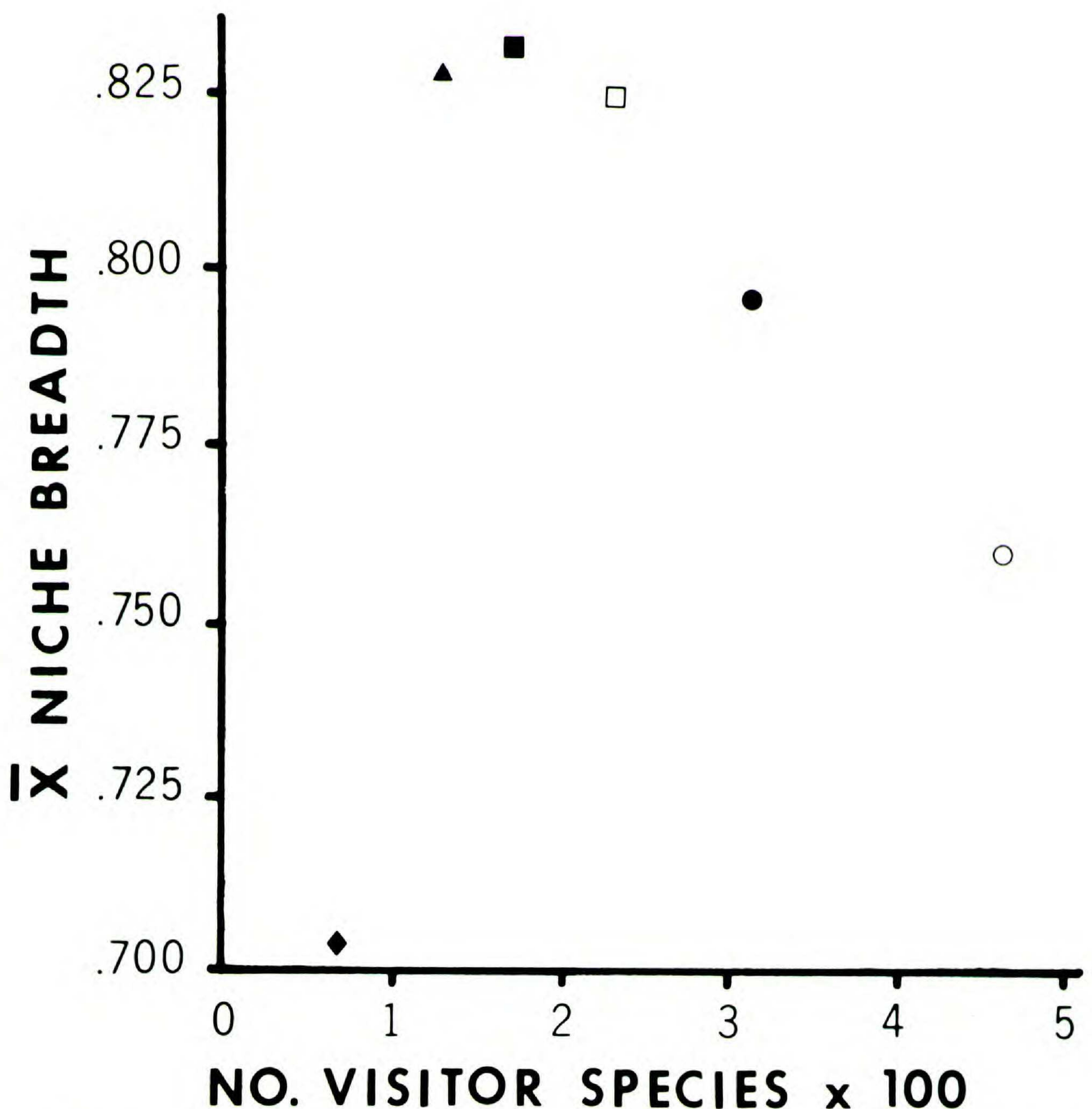


FIGURE 3. Correlation between the number of species and the mean niche breadth of common flower-visitor species in a community. \blacklozenge = Area P; \blacktriangle = Area S; \blacksquare = Area G, dry season; \square = Area G, wet season; \bullet = Area E, dry season; \circ = Area E, wet season.

the proportion of oligolectic bees increased as species diversity increased among communities in California.

This pattern did not extend to the very different habitat of the shrubby Montane Rain Forest (Area P), as the niche breadths of flower-visitors tended to be much narrower than predicted. This may have resulted from a relatively constant temperature stress in the high altitude environment. The mean annual temperature near Area P was only 10.8°C , and the range in monthly means was 9.6°C to 11.8°C (Holdridge *et al.*, 1971). These low temperatures, with no real warm season, may have resulted in large energetic stresses on invertebrates, especially flower-visitors which need energy to fly from flower to flower (Heinrich, 1972). There is just one abundant generalist species in Area P, *Bombus ephippiatus*. The genus *Bombus* is able to regulate body temperature to a large degree. Most of

TABLE 2. Mean niche overlap values, the number of species-pairs values, and number of species.

Area	\bar{X} Overlap	N ^a	No. Species ^b
S	.2871	91	138
G _{dry}	.2840	77	175
P	.1968	141	69
G _{wet}	.1966	50	217
E _{dry}	.1870	404	318
E _{wet}	.1644	636	462

^a "N" = the number of species pairs used in calculating the mean overlap. Only species represented by more than 11 individuals were included in the niche overlap analysis.

^b No. Species = the total number of flower visitor species in each area.

the remaining, relatively non-thermoregulating, species visit just one or two *Senecio* species. These are patchy and offer a large amount of resource per patch. Specialization on patchy resources could clearly be advantageous where temperatures are low (Heinrich & Raven, 1972). With many species utilizing a few, patchy resources it appears that temperature stress creates an environment that consists of a series of refugia for most flower-visitor species. That is diversity in Area P may depend more on the presence of concentrated resources than on changes in niche breadth. Cruden (1972) also found evidence for the restriction of bee activity at high altitudes. Therefore we can see that changes in niche breadth follow predictions within similar climatic zones, but they may differ from predictions as temperature stress becomes extreme.

NICHE OVERLAP

For the lowland communities there is a minor trend toward decreasing niche overlap with increased species packing (Table 2). This could be the result of the decrease in niche breadth that was observed with increasing species numbers. Increasing niche overlap is not an important mechanism for controlling species packing in the Costa Rican communities. This conclusion is consistent with the predictions of May and MacArthur (1972), which were based on MacArthur's model of regulation of diversity through competition. In this paper they assert that niche overlap should not increase greatly through broad ranges of environmental variation.

RESOURCE DIVERSITY

The number of visitor species in a study area each month was positively correlated with floral diversity. This relationship held for all communities when floral diversity was expressed as number of species (Fig. 4) (Pearson product-moment correlation, $r = .7588$, $P < .01$). The number of lowland visitor species was also positively correlated with floral resource abundance (Fig. 5) ($r = .5710$, $P < .01$), and this is precisely the relationship predicted by the competition theory of diversity regulation. Consumer diversity should increase with resource diversity. Area P did not follow this trend, because the number of visitor species

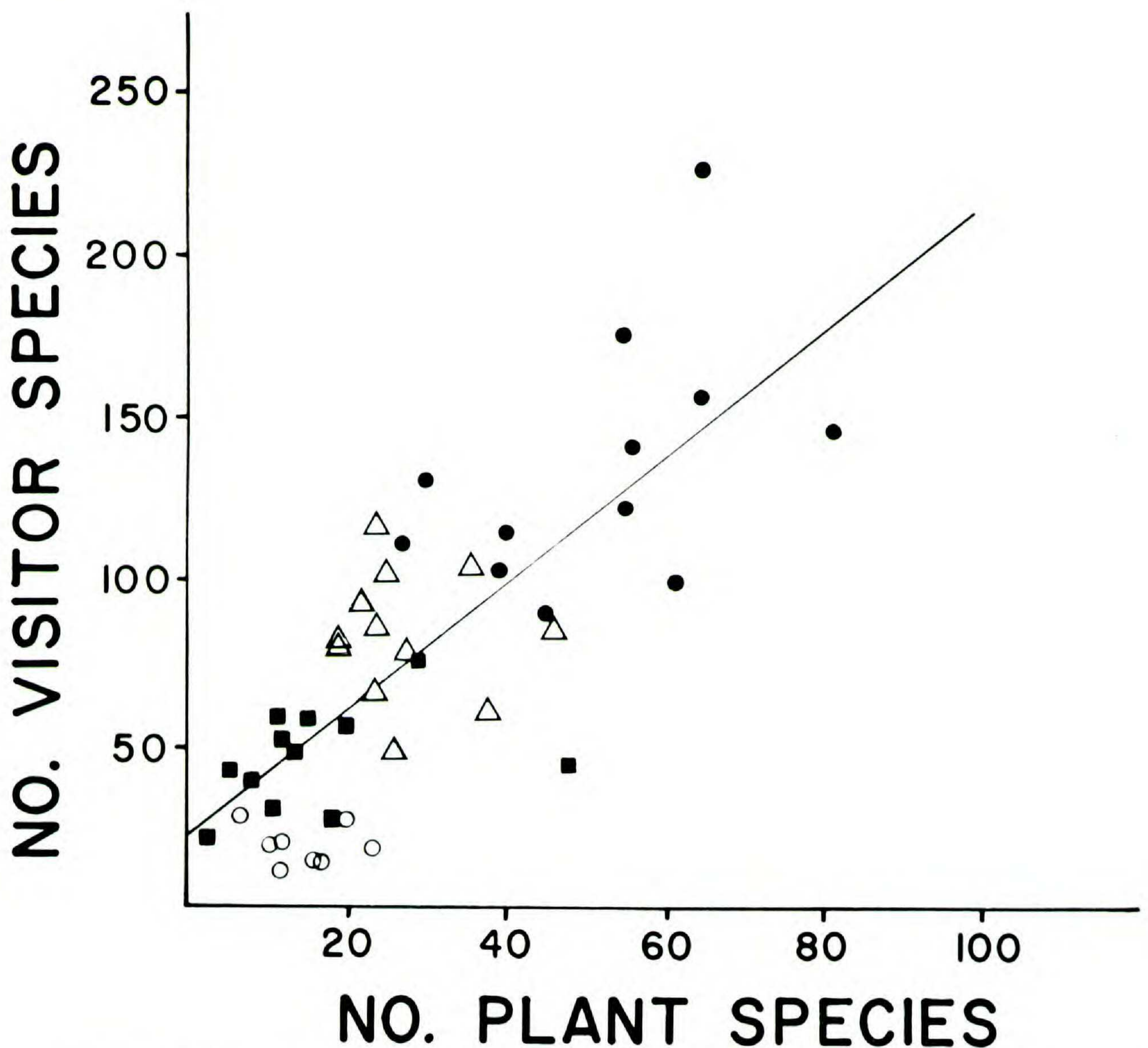


FIGURE 4. Correlation between the number of visitor species and plant species in monthly censuses in each area. ■ = Area S; ○ = Area P; △ = Area G; ● = Area E. The correlation is significant, $r = .7588$. $P < .01$.

was more closely associated with a few, often relatively uncommon, but patchy plants such as *Senecio oerstediana*.

In summary, the competition theory of diversity regulation generates predictions that are confirmed by observations in lowland, seasonal tropical communities. Niche breadth decreases as the number of species in a community increases, and species diversity increases with increasing resource diversity. Changes in niche overlap probably do not contribute to increased diversity, but the observed differences in niche overlap can be explained by differences in the average niche breadth in communities. Observations from a high altitude site do not confirm predictions based on the competition theory and data from lowland areas. Average niche breadth is much lower than predicted, and the number of visitor species is lower than predicted by the abundance of floral resources. Additional parameters, such as environmental severity, may be needed to supplement competition theory in explaining diversity differences in extreme environments. However, the competition theory is nicely supported by lowland community results,

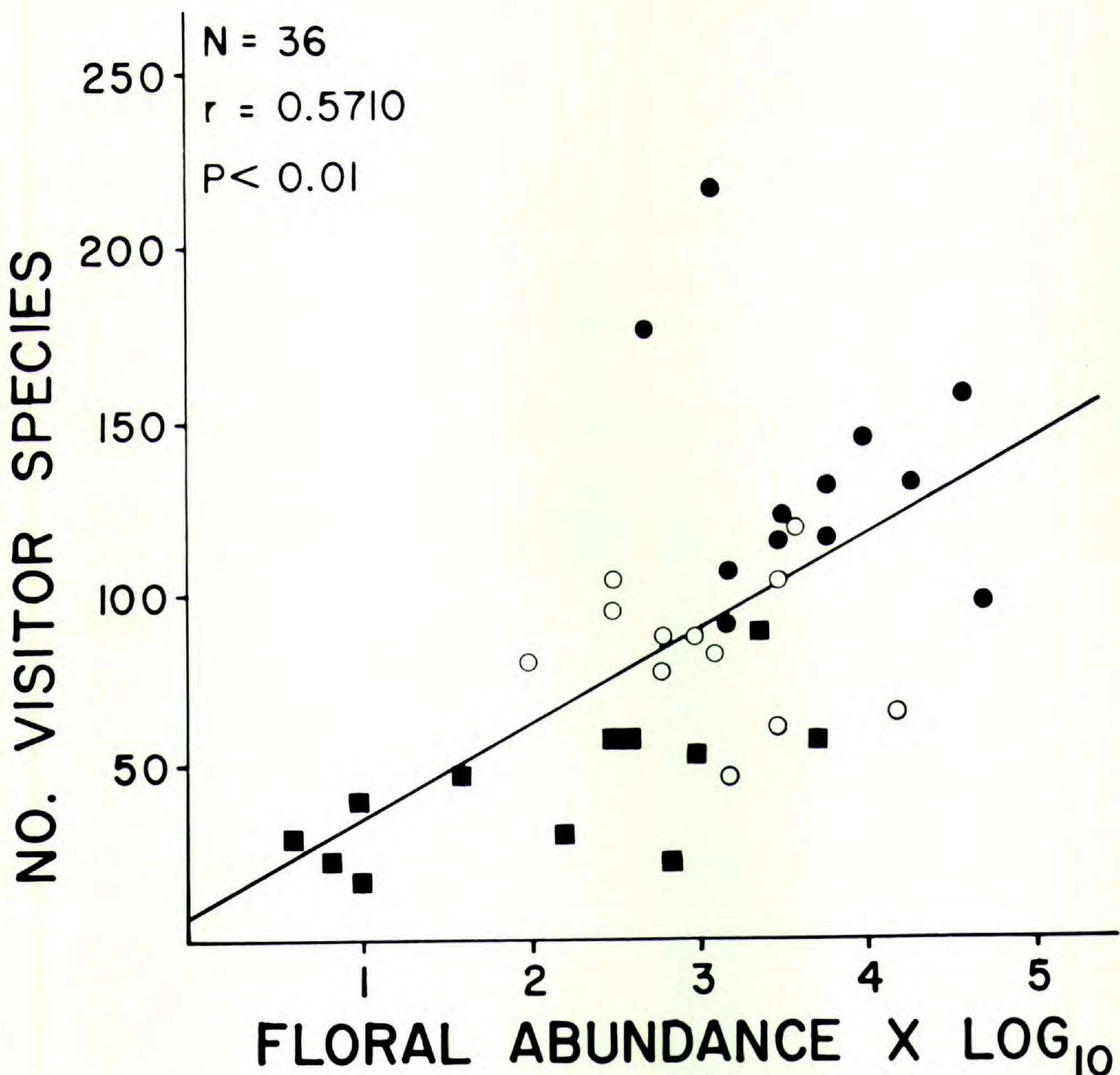


FIGURE 5. Correlation between the number of visitor species and floral abundance in monthly censuses in lowland areas. ■ = Area S; ○ = Area G; ● = Area E.

and the structure of these flower-visitor communities can be directly related to plant-animal interactions. Pollination systems are important at the community level of organization as well as at the level of species-species coevolution.

COMPETITION FOR POLLINATOR SERVICES

The idea that plants compete for pollinator services must be nearly as old as the observation that different flower types attract different visitors. The mechanisms of this competition have been studied in some systems with a few competing species (Free, 1968; Levin & Anderson, 1970; Levin, 1972a, 1972b). There have also been assertions that competition for pollinators is not confined to a few or closely related species, but that it is a major factor in the evolution of the timing of flowering within entire plant communities (Hocking, 1968; Croat, 1969; Mosquin, 1971). The implications of the latter claim are different than those arising from knowing that two, or a few, species are competing for polli-

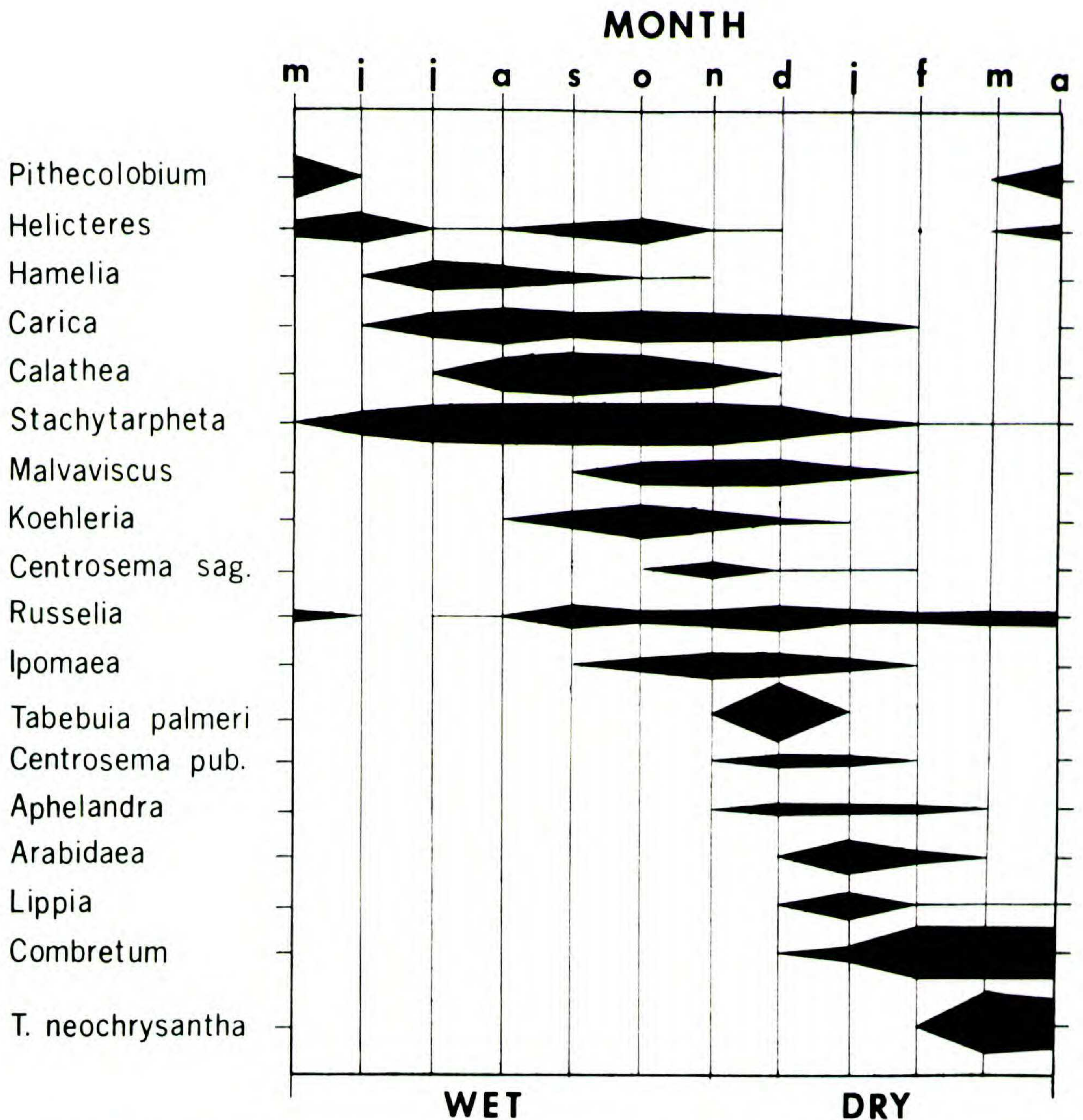


FIGURE 6. Temporal distribution of floral abundance of "butterfly-pollinated" plants. The vertical axis for abundance uses a \log_{10} scale. The range of the wet and dry seasons is given.

nators. In two species systems competition for pollinators could result in subspeciation, in the extinction of one of the species, or selection for the displacement of flowering periods. If competition for pollinators operates on a community level, then it is possible that all potential flowering periods would be used in diverse communities. In such saturated communities no additional flowering plants could become established, if they required animal-mediated pollination. Claiming competition for pollinators on a community level therefore implies interactions. This is in contrast to the belief that present plant communities "could soak up many more species" (Whittaker, 1969; Ross, 1972), so the assertion of competitive displacement of flowering should be critically examined.

Naturally, experimental methods have not been used to determine that competition for pollinators affects large communities. Such techniques would be

TABLE 3. The number of species in flower and the distribution of flowering peaks^a through time in a complex deciduous forest.

Pollinator Syndrome	Month											
	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	IV
Large Bees:												
Number of Peaks	3	4	2	3	4	3	9	4	3	4	4	2
Number of Species	7	10	6	10	9	12	14	12	12	11	9	10
Small-medium Bees: ^b												
Number of Peaks	7	2	1	4	7	4	8	9	6	3	1	1
Number of Species	10	9	7	13	16	17	18	24	18	14	6	10
Wasps:												
Number of Peaks	3	2	0	0	1	1	2	0	2	2	0	1
Number of Species	4	2	0	2	2	4	3	0	2	3	1	3
Hummingbirds:												
Number of Peaks	1	1	1	1	3	2	4	6	3	1	2	1
Number of Species	4	3	3	6	7	8	9	10	10	8	4	7
Butterflies:												
Number of Peaks	2	2	2	3	3	2	2	2	3	0	0	3
Number of Species	3	6	5	10	9	9	10	8	9	7	5	6

^a A "peak" = a month in which the floral abundance for a species is at or within 25 percent of its maximum.

^b The distributions of numbers of "small and medium bee flower" species in bloom and peak flowering periods are the only distributions that differ significantly from an evenly spaced pattern (Chi-square Test).

impractical; so indirect evidence again has been used. This hypothesis was supported by Mosquin's (1972) studies of northern Canadian communities. Here, dominant species that offered large floral rewards appeared to "displace" the flowering periods of plants that offered less floral resource.

The remaining line of evidence that competition for pollinators involves whole plant communities comes from studies of flower phenology. A frequent pattern emerging from phenology is a temporal displacement of flowering for species with similar pollination syndromes, so that some species are blooming throughout the growing period (Croat, 1969; Mooney *et al.*, 1973; Heithaus *et al.*, 1973). I found similar "displacement" of flowering times in Area E, the complex, lowland, deciduous forest (the other communities have not yet been similarly analyzed). The flowering periods of "butterfly-pollinated" and "hummingbird-pollinated" plants are shown in Figures 6 and 7. I found nearly the same number of plant species in bloom and the same number of species reaching peak flower production each month. These distributions were not significantly different than ones predicted by assuming an "even" distribution of flowering through the year (Chi-square Test), except for the plants in the "small-medium sized bee syndrome" (Table 3).

One of the big problems with this analysis is the large amount of overlap in flowering periods. If competition for pollinators were important, nearly non-overlapping flowering periods would be expected. Secondly, the observed flowering pattern is also the one predicted by assuming that flowering periods are

determined purely at random. Demonstrating the "displacement" of flowering periods is one problem, but linking the pattern to competitive interactions and explaining the overlap is quite a different one.

If we temporarily assume that competition for pollinators is important, we can generate at least two testable hypotheses. First, plants that bloom simultaneously should have different visitor species; or if the same visitors are attracted, then one or two plant species would probably "outcompete" the others (Levin & Anderson, 1970). To test this prediction I looked at visitation patterns among plants in two pollination syndromes—butterfly- and hummingbird-pollinated plants. These were chosen on the basis of the relatively small numbers of species involved and ease of analysis. Some generalist plants (those attracting and potentially pollinated by several vector types) were included in both syndromes. First I determined the total number of visits to flowers made by hummingbirds or butterflies, combining visits to all plant species. Secondly, two visitation characteristics were determined for each plant species in a syndrome: (1) the most common visitor species (primary visitor), and (2) the proportion of total visits received by the single plant species. Plants receiving fewer than 5 percent of the total visits for the syndrome were noted.

Butterfly-pollinated plants tended to have different primary visitors, if the plants were visited frequently. Sixty-eight percent ($N = 22$) of the infrequently visited plants shared primary visitors with a frequently-visited plant. Just two wet season plants were equally successful in attracting one "primary" pollinator species (Table 4). The butterfly was extremely abundant in the area, and there was no overlap in the less common butterfly species that visited these two plants, *Cordia* sp. 2 and *Tridax procumbens*. Thus, overlap in visitors was not extensive in this case. During the dry season only two commonly visited species (*Tridax*, *Melanthera aspera*) appeared to share visitor species (Table 5). Their "primary" visitor, *Eurema diara*, was extremely abundant, and again, there was little overlap in the less common butterflies that visited the two plants.

There were even fewer cases of overlap in common visitor species to hummingbird-pollinated plants (Fig. 7). As in butterfly-pollinated plants, when two plants were visited by the same "primary" visitor one, of them received fewer than five percent of the observed visits. This result is especially interesting when we consider the fine temporal adjustments flowering plants can make. Compared to potential differences in daily anthesis, differences in monthly flowering reflect a very coarse time scale. That we encounter so few exceptions to a prediction based on monthly flowering is impressive. It is fair to say that the prediction based on the hypothesis that these species are dividing the pollinator resources is supported by the analysis of visitation frequencies to simultaneously blooming plants.

Other predictions can be made. For example, if competition is important at the community level, then regulation of floral diversity may fit MacArthur's (1972) conceptualization. Floral diversity (although not necessarily plant diversity) would depend on the diversity of available pollinators, the average specialization of flowers, and the average "pollinator-niche"-overlap in a community.

TABLE 4. Visitation patterns to "butterfly-pollinated" plants.

Plant Species	Month											
	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	IV
<i>Casearea</i> n. sp.	(Me) ^{b, c}											
<i>Cordia</i> sp.	Me											
<i>Cordia pringlei</i>	Hh ^c											
<i>Matelea</i>			(Hh)	Hh	Hh	Hh						
<i>Hamelia</i>			(Hh)	(Hh)	(Hh)							
<i>Carica</i>			NV ^a	NV	NV	NV	(Hh)	(Hh)	NV			
<i>Lonchocarpus</i>				NV								
<i>Tridax</i>	Me + Ed ^c	Me + Ed	Me + Ed	Me + Ed	Me + Ed	Ed			Py ^c + Ed	Py + Ed	Ed	Ed
<i>Cordia polyceph.</i>					Zo ^c	Zo	Zo					
<i>Stachytarpheta</i>		Ur ^c	Ur	Ur	Ur	Ur	Ur	Ur				
<i>Hyptus</i>					(Ur)	(Ur)	(Ur)	(Ur)	(Ur)			
<i>Callicophyllum</i>							Ad ^c	Ad	He ^c			
<i>Melanthera</i>							Ed	Ed	Ed	Ed	Ed	Ed
<i>Licania</i>									Af ^c			
<i>Cupania</i>									Vs ^c	Vs		
<i>Lantana</i>	(Hh)	(Hh)	(Hh)	(Hh)	(Hh)	(Hh)	(Hh)	(Hh)	(Hh)	(Ed)	(Ed)	(Ed)
<i>Asclepias</i>		Af	Af	Af	Af	Af	Af	Af			Af	Af
<i>Blechnum</i>												(Ed)

^a NV = not visited.^b () indicate that less than 5 percent of all butterfly visits were to the plant listed.^c The most common butterfly visitors are indicated by the following abbreviations: Ad = *Adelpha* sp., Af = *Anartia fatima*, Ed = *Eurema diara*, He = *Hesperidae*, Hh = *Heliconius hecale*, Me = *Microtia elva*, Py = *Pyrgus* spp., Ur = *Urbanus* spp., Vs = *Victorina stelenes*, Zo = *Zopyrion* sp.

TABLE 5. Visitation patterns to "Hummingbird-pollinated" plants.

Plant Species	Month											
	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	IV
<i>Pithecolobium</i>	NV ^a				(AR)	(AR)						NV (AR)
<i>Helicteres</i>	(AR) ^{b, c}	(AR)										
<i>Hamelia</i>		AS ^c										
<i>Carica</i>					NV	NV	NV	He ^c	He			
<i>Calathea</i>					AS	AS	AS			He		
					+	+	+					
				Pl ^c	Pl	Pl	Pl					
<i>Stachytarpheta</i>		AR	AR	AR	AR	AR	AR	AR	AR			
<i>Malcaviscus</i>					(AR)	(AR)	(AR)	(AR)	(AR)			
<i>Koehleria</i>					Hy	Hy	Hy	Hy	Hy			
<i>Centrosema sag.</i>												
<i>Russelia</i>	NV				NV	NV	NV	(AS)	NV	NV	NV	NV
<i>Ipomaea</i>						(AS)	(AS)	(AS)	(AS)			
<i>Tabebuia palmeri</i>							NV	NV	NV			
<i>Centrosema pub.</i>							NV	NV	NV			
<i>Aphelandra</i>							NV	NV	NV			
<i>Arabidaea</i>							(HC) ^c	(HC)	(HC)			
<i>Lippia</i>							(AS)	(AS)	(AS)			
<i>Combretum</i>							AS	AS	AS			AS
<i>T. neochrysantha</i>												AS (HC) +
												(AS)

^a NV = not visited.^b () indicate that less than 5 percent of all hummingbird visits were to the plant listed.^c The most common hummingbird visitors are indicated by the following abbreviations: Ar = *Amazilia rufila*, As = *A. saucerotti*, Hc = *Heliothra constantii*, He = *Hylocharis eliciae*, Hy = *H. sp. 2*, Pl = *Phaethornis longuemareus*.

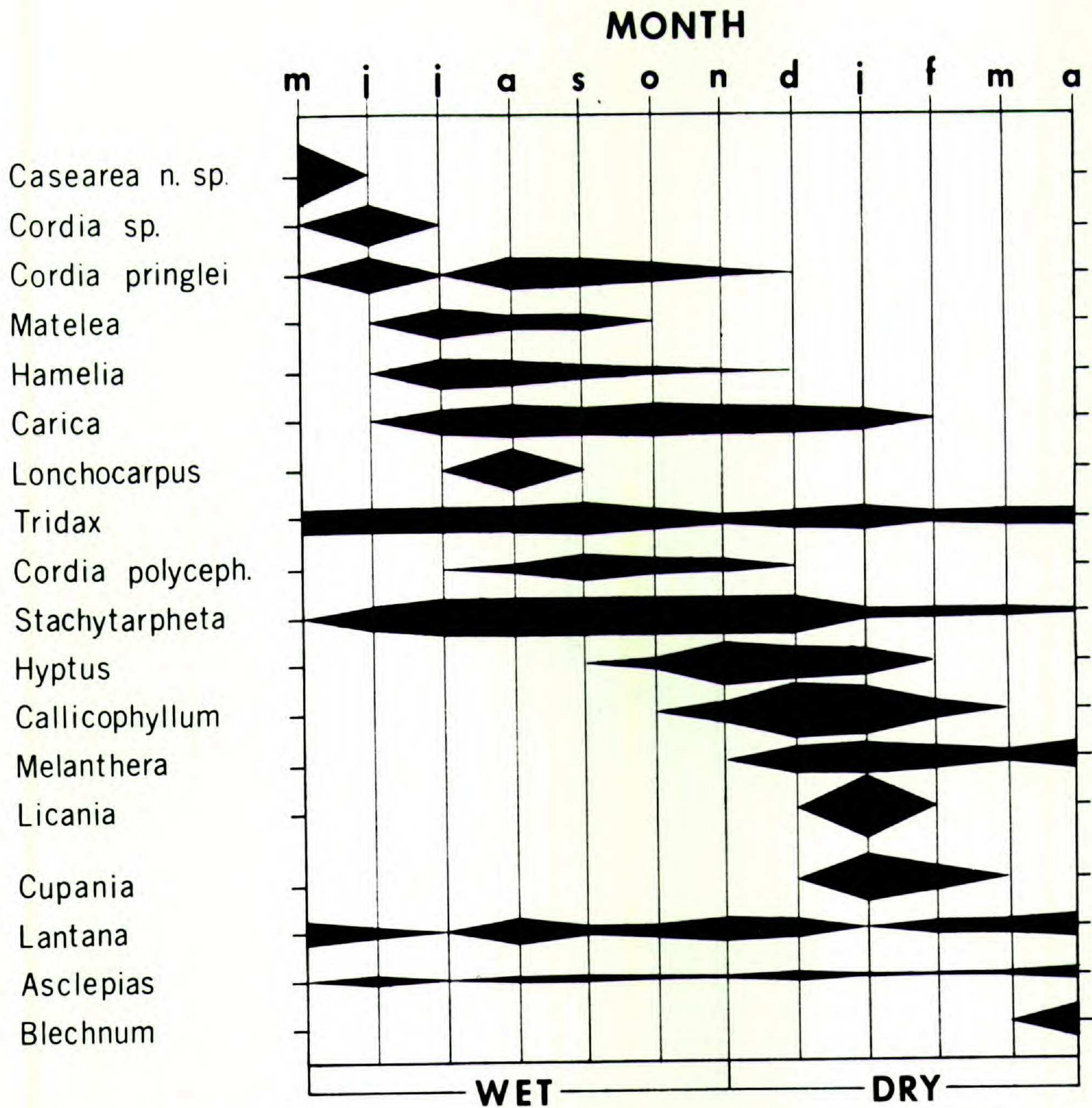


FIGURE 7. Temporal distribution of floral abundance of "hummingbird-pollinated" plants. The axis are as in Figure 6.

There are hints that this prediction will be confirmed. We have already noted the correlation between floral diversity and flower-visitor diversity. We must refine our analysis to distinguish the truly potential pollinators among nectar and pollen consumers. Further analysis of visitation to Costa Rican plants, combined with Moldenke's and Raven's studies, should allow an evaluation of this prediction.

To conclude, there is evidence from lowland Costa Rican communities that plant-animal interactions at flowers are very important to the determination of community structure. The diversity of flower-visitors is largely a function of competition for floral resources, and in turn, the diversity regulation through competitive interactions, diversity in these communities should be at equilibrium. We would not expect major increases or decreases in species diversity through "ecological" time. However, if this is essentially a positive-feedback system,

where increased floral diversity increases flower visitor diversity, and increased pollinator diversity increases floral diversity, we must wonder whether there are any limits to diversity through evolutionary time. Perhaps limits to potential productivity would impose a ceiling on floral resource diversity, but for the present this remains an open question. At the very least we can conclude that plant-animal interactions at flowers are an important and interesting component of community structure and that these interactions deserve more attention in community studies.

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